

Killer storms: North Atlantic hurricanes and disease outbreaks in sea urchins

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Abstract

An increase in the incidence of disease in various marine organisms over the past few decades has been linked to ocean climate change. In Nova Scotia, Canada, mass mortalities of sea urchins, due to an amoebic disease, are associated with tropical cyclones of relatively high intensity that pass close to the coast when water temperature is above a threshold for disease propagation. These conditions increase the likelihood of introduction and spread of a nonindigenous water-borne pathogen through turbulent mixing. Our analysis shows that the most deadly storms, in terms of the probability of a sea urchin mass mortality, have become more deadly over the past 30 years. We also found that storms have been tracking closer to the coast and that surface temperature has increased during the hurricane season. These trends are likely to continue with climate warming, resulting in a regional shift to a kelp bed ecosystem and the loss of the urchin fishery.

The frequency and severity of disease outbreaks appear to be increasing in a broad range of marine taxa (Harvell et al. 1999; Lafferty et al. 2004). This trend has been attributed to escalating anthropogenic stressors and changes in the ocean environment over the past several decades and is predicted to continue with climate warming (Harvell et al. 2002; Mydlarz et al. 2006). When epidemics cause declines in ecologically or economically important species, such as seagrass, shellfish, corals, or marine mammals, disease can alter the structure and functioning of whole ecosystems, as well as the goods and services provided to humans (Lafferty et al. 2004). The need to understand the mechanistic links between climate change and temporal and spatial trends in disease outbreaks is increasingly urgent, particularly in view of our limited ability to mitigate disease in the ocean (McCallum et al. 2003; Ward and Lafferty 2004).

Diseases that affect herbivorous sea urchins (Tajima and Lawrence 2001) provide striking examples of the cascading effects of population declines in an ecologically important group. Disease appears to have increased in sea urchins worldwide (Ward and Lafferty 2004), and catastrophic mortalities have caused major transitions in community state (or phase shifts) in tropical coral reefs (Lessios 1988; Hughes 1999) and temperate kelp forests (Lauzon-Guay et al. 2009; Uthicke et al. 2009). On the Atlantic coast of Nova Scotia, Canada, recurrent outbreaks of an amoebic disease of the green sea urchin *Strongylocentrotus droebachiensis* have been documented since 1980 (Scheibling and Hennigar 1997; Miller and Nolan 2008). Evidence from field observations and laboratory experiments suggest the pathogenic agent *Paramoeba invadens* (Jones and Scheibling 1985) is a nonindigenous species, delivered episodically to this coast by large-scale advective processes (Scheibling and Hennigar 1997). Turbulent mixing by tropical cyclones (hurricanes) has been proposed as a potential mechanism for transport of planktonic amoebae across the Scotian Shelf (Scheibling and Hennigar 1997),

and mass mortalities of sea urchins were observed following recent hurricanes that made landfall or passed close to Nova Scotia (Scheibling et al. 2010).

In this study, we examine links between sea urchin mass mortality events, hurricane activity, and water temperature (which mediates disease outbreaks) on the Atlantic coast of Nova Scotia over a 30-yr period (1980–2009). We apply logistic regression techniques that show the probability of mass mortality is related to the intensity and proximity of tropical cyclones along this the coast, hypothesized to deliver the pathogenic agent, and is related to ocean temperatures that favor the propagation of disease. We also show that the likelihood of deadly storms for sea urchins has increased over this 30-yr period, a trend we expect will accelerate with future climate warming.

Methods

Sea urchin mass mortality—We compiled a record of sea urchin mass mortality along the Atlantic coast of Nova Scotia since 1980, based on reports in the scientific literature or interviews with sea urchin harvesters (see Web Appendix, www.aslo.org/lo/toc/vol_55/issue_6/2331a.html). We define a mass mortality event as one in which a large proportion of sea urchins (usually > 50% and up to 100%) inhabiting the rocky subtidal zone above 25-m depth (a limit determined by the temperature threshold for progression of disease; Scheibling and Stephenson 1984) succumb to paramoebiasis either locally (e.g., within a large embayment) or on a coastal scale. In some years, mortality in the shallow subtidal zone was nearly complete across hundreds of kilometers of coastline (linear distance), while in other years the disease was arrested by declining temperatures, leaving enough surviving urchins to maintain the barrens state (Miller 1985a; Scheibling and Hennigar 1997). We do not consider the spatial extent of mortality in designating years with mortality events because factors affecting the spread of the disease may differ from those that trigger an outbreak.

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For each event, overt signs of paramoebiasis, which distinguish this disease from bacterial and macroparasitic infections of *S. droebachiensis* (Tajima and Lawrence 2001; Roberts-Regan et al. 1988), were observed in situ by scientists or sea urchin fishers familiar with the disease (*see* Web Appendix). Strong wave forces, such as those that accompany tropical cyclones, are neither a direct nor indirect (by causing damage that increases susceptibility to disease) cause of these mass mortalities, since sea urchins respond to increased wave action by sheltering in protective microhabitats (Lauzon-Guay and Scheibling 2007). For example, we did not observe unusual mortality, damage, or dislodgment of *S. droebachiensis* immediately after Hurricane Bill in 2009; the first signs of paramoebiasis appeared 3 weeks later and culminated in near complete mortality of urchins (Scheibling et al. 2010).

These catastrophic mortalities are conspicuous events, resulting in large numbers of moribund urchins and intact tests deposited on the seabed or cast upon the shore. Given the rapid transmission and progression of paramoebiasis at temperatures exceeding the threshold (Scheibling and Stephenson 1984), it is unlikely that the disease occurs at low prevalence in some years, causing a low level of mortality that escapes detection by scientific divers or sea urchin harvesters.

Storm tracks and intensity—To examine the possible link between disease outbreaks that cause sea urchin mass mortality and tropical cyclones in the North Atlantic, we obtained “best track” data on individual storms (hurricanes and tropical, subtropical, and posttropical storms) between 1980 and 2009 from the Unisys weather database (<http://weather.unisys.com/hurricane/atlantic/index.html>). Data files contained 6-hourly storm center locations (latitude and longitude), maximum 1-min surface (10 m) wind speeds (knots). Wind speeds were converted from knots to kilometers per hour for analysis. Only tropical storms and posttropical storms that passed between 35°N and the Atlantic coast of Nova Scotia (maximum latitude: 47°N), and between 55 and 70°W, were included in our analyses (*see* Web Appendix, Fig. 1).

For each storm, we calculated the minimum distance between the coast and the storm center based on the position of the storm at 6-h intervals and recorded the maximum sustained wind speed (km h^{-1}) at that time and position. Minimum distance from the coast (km) was measured as the shortest straight line between the storm center and a series of seven points spaced at 100-km intervals along the Atlantic coast from Cape Sable Island (44°14'N, 64°12'W) at the southwestern tip of Nova Scotia to Scatarie Island (46°01'N, 59°40'W) at the eastern tip of Cape Breton Island. Storm coordinates (latitude and longitude) and maximum sustained wind speeds recorded at that time were used in our analyses.

Water temperature—Laboratory studies show that progression of paramoebiasis in sea urchins is strongly temperature dependent (Scheibling and Stephenson 1984; Jellett and Scheibling 1988). This enabled us to link mortality events to candidate storms that preceded them

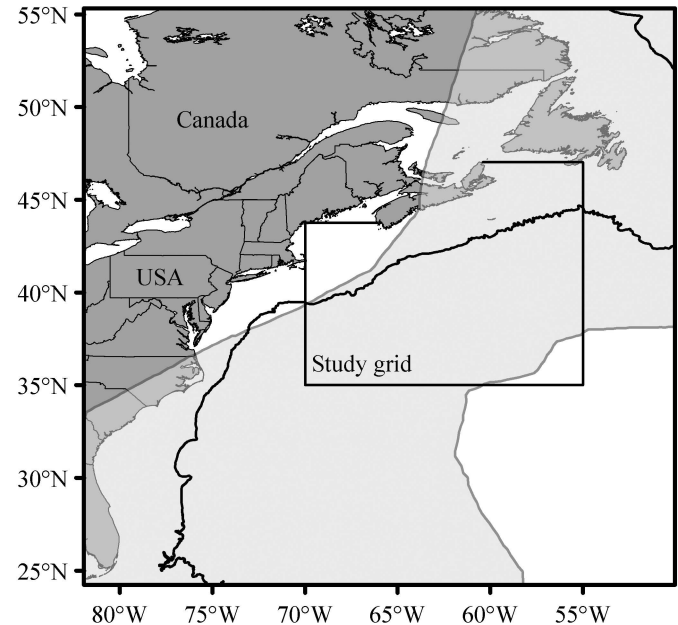


Fig. 1. Map of western North Atlantic showing the edge of the continental shelf (solid line) and the study grid (box) off the coast of Nova Scotia. Shaded area encompasses the tracks of 12 candidate storms between 1980 and 2009.

by estimating the expected time to 50% morbidity (t_{50} , d) based on the average ocean temperature (T , °C) over the 2-week period following each storm, using the equation: $t_{50} = 23492T^{-2.7476}$ (Scheibling et al. 2010). A 2-week interval encompassed the expected time for sea urchins to develop symptoms of paramoebiasis at temperatures (14–16°C) that typically precede disease outbreaks; sea urchins exhibiting these symptoms typically die within 1–2 d (Scheibling and Stephenson 1984; Scheibling and Hennigar 1997). The disease does not develop in sea urchins below a threshold temperature of $\sim 10^\circ\text{C}$ (Scheibling and Stephenson 1984), and t_{50} was not calculated for storms occurring when the average poststorm temperature was below this threshold.

Average daily water temperature between 1980 and 2008 was obtained from the Coastal Time Series (CTS) database (<http://www.mar.dfo-mpo.gc.ca/science/ocean/database/Doc2003/cts2003app.html>) for thermographs at 0–10-m depth located within a polygon along the central coast of Nova Scotia, extending from Halifax Harbour (44°39'N, 63°34'W) to Lunenburg Bay (44°15'N, 64°14'W) and 5 km offshore. CTS temperature data were not available for 2009, when temperatures were obtained from a single thermograph at 8-m depth at the site of a sea urchin mass mortality in St. Margarets Bay, Nova Scotia.

Model development—Sea urchin mass mortality has been recorded on the Atlantic coast of Nova Scotia in 13 of 30 years since 1980 (*see* Web Appendix). In 12 of these years, the mortality event was preceded by a tropical cyclone. In the remaining year (1983), experiments that incidentally or deliberately released *P. invadens* into Halifax Harbour and on the southern shore of Cape Breton Island, Nova Scotia (Miller 1985b; Jellett and Scheibling 1988; Jellett et al. 1989), may have caused the widespread mass

Table 1. Comparisons of logistic models ($P_m = 1/(1 + e^{-z})$) fit to sea urchin mass mortality events between 1980 and 2009. AICc is Akaike's information criterion with a second-order correction for small sample size. Δ AICc is the difference in AICc between each model and the model with the best fit (model 1). Model 2 is used to calculate temporal trends in the probability of a sea urchin mass mortality (P_m) as a function of storm characteristics only. Wind is the maximum sustained wind speed (km h^{-1}), Dist^2 is the squared minimum distance from the Nova Scotia coast (km), and Temp is the dummy variable for the temperature threshold (12.2°C).

Model	Parameters	AICc	Δ AICc
1 $z = \beta_0 + \beta_w \times \text{Wind} + \beta_d \times \text{Dist}^2 + \beta_t \times \text{Temp}$	4	40.45	
2 $z = \beta_0 + \beta_w \times \text{Wind} + \beta_d \times \text{Dist}^2$	3	49.93	9.48
3 $z = \beta_0 + \beta_w \times \text{Wind} + \beta_t \times \text{Temp}$	3	52.05	11.60
4 $z = \beta_0 + \beta_w \times \text{Wind}$	2	58.19	17.74
5 $z = \beta_0 + \beta_t \times \text{Temp} + \beta_d \times \text{Dist}^2$	3	64.89	24.44
6 $z = \beta_0 + \beta_t \times \text{Temp}$	2	65.40	24.95
7 $z = \beta_0$	1	70.82	30.37
8 $z = \beta_0 + \beta_d \times \text{Dist}^2$	2	71.83	31.38

mortality that fall (Miller 1985a). Based on the onset of mass mortality and the estimated t_{50} following the passage of each storm, we identified candidate storms for the mortality event in each of the 12 years (*see* Web Appendix). In nine of these years, two to four successive storms were possible candidates based on records of poststorm water temperature and timing of the observed mass mortality (notably in 1996, 2000, and 2001 when mortality records were temporally imprecise).

We used a logistic regression model to estimate the expected probability of a mass mortality (P_m) associated with each storm between 1980 and 2009. Presence or absence of mass mortality was the dependent variable in this model, and maximum sustained wind speed, minimum distance from coast, and a threshold water temperature were independent variables. We applied log, square root, and square transformations to the wind speed and distance variables; only the square of distance provided a better fit to the model than untransformed data. Water temperature was added as a dummy variable to emulate a threshold below which mass mortalities do not occur, with a value of 1 for temperatures above a threshold value and a value of 0 for temperatures below the threshold. The optimal threshold value was selected by rerunning the logistic regression model for threshold values ranging from 9°C to 14°C in 0.1°C increments and selecting the value (12.2°C) that resulted in the best fit of the model to the data. First- and second-order interactions among independent variables also were added to the model, but these did not increase the fit to the data, and we excluded them from our analysis.

We selected the best model based on Akaike's information criterion (Burnham and Anderson 2002) using SAS Release 8.02 (SAS Institute) (Table 1). Because we could not identify a unique candidate in some years, we ran the regression model iteratively, using all possible combinations of candidate storms (one per year for each of the 9 yr with alternatives) to obtain the set of storms that provided the best fit to the model. In this way, we allowed the model to select among alternative candidate storms. For final parameter estimation, we excluded from our analysis any storm occurring after the selected candidate storm, or the onset of mass mortality in a particular year,

because we could not assess whether such storms contributed to the mortality event. Our selection of a single storm presents a conservative estimate of the probability of mass mortality, since more than one candidate may have delivered the pathogen or multiple storms may have acted synergistically in doing so.

To assess whether randomly selecting candidate storms could result in a similar fit to the logistic regression model, we conducted a Monte Carlo analysis. We ran 100,000 logistic regressions and randomly selected 12 storms to be associated with a mass mortality from all storms. We compared the distribution of the fit of the logistic model, assessed using the deviance ($-2 \log$ -likelihood), with the fit obtained with our candidate storms and calculated the probability of obtaining a better fit (smaller deviance) using randomly selected storms.

Trend analysis—To examine the trend in the expected probability of a mass mortality of sea urchins (P_m) associated with each tropical cyclone approaching Nova Scotia since 1980, we used a reduced model (Table 1), including the parameters specific to the storms themselves (wind speed and distance from the coast) and excluding a temperature threshold, to calculate P_m . We used quantile regression analysis (Koenker 2005), based on the software package “quantreg” (quantreg: Quantile Regression, R package version 4.30) in R, to detect temporal trends in P_m , as well as trends in storm characteristics (wind speed, distance from coast) and environmental conditions (water temperature). Because only a small number of storms occur within each year, we pooled storms in 3-yr groups to increase the sample size used to calculate quantiles. For each parameter, we used least-square regression to evaluate the trend in the median, the 75th quantile, and 1.5 times the interquartile range. We also measured the trend for every five-quantile interval between the 5th and 95th quantile and the respective 90% confidence intervals.

Results

Probability of mass mortality associated with storm events and ocean temperature—The best model to predict storms

Table 2. Parameter estimates of model 1 and 2 (Table 1) with standard error from logistic regression analysis.

Parameter	Estimate	SE
Model 1		
β_0	-14.352	4.526
β_w	0.082	0.025
β_d	-0.069	0.026
β_t	4.966	2.113
Model 2		
β_0	-7.763	1.949
β_w	0.059	0.017
β_d	-0.045	0.019

associated with mass mortalities of sea urchins included all of our designated independent variables: maximum sustained wind speed, distance from the coast (squared), and a water temperature threshold (12.2°C) (Tables 1 and 2). Storms with high wind speed and short distance from the coast have a higher probability of being linked to a mortality event than other storms (Fig. 2). Our candidate storms had wind speeds $> 111 \text{ km h}^{-1}$ and were within 535 km of the coast (Fig. 2). The average wind speed of candidate storms ($138.2 \pm 6.8 \text{ SE km h}^{-1}$) was significantly greater than that of other storms ($95.8 \pm 3.2 \text{ km h}^{-1}$) ($t_{105} = 4.486$, $p < 0.001$). Candidate storms, on average, also approached closer to the coast ($346.7 \pm 51.5 \text{ km}$) than other storms ($470.2 \pm 35.5 \text{ km}$), although this difference was marginally significant ($t_{25} = 1.975$, $p = 0.060$). Storms preceding periods when average water temperature was above 12.2°C had an greater probability of being linked to a mortality event than other storms (Fig. 2). Only one of the 12 storms associated with sea urchin mortality occurred when water temperature was below this threshold (Hurricane Debby, 11.2°C ; see Web Appendix, Fig. 2B).

Our Monte Carlo analysis showed that none of the random iterations of the logistic regression gave a better fit than our candidate storms. In other words, our candidate storms, based on the estimated time to mass mortality, are more distinct (in terms of wind speed and distance from the coast) from other storms than any of the 100,000 randomly selected sets storms.

Trend analysis—Our trend analysis showed that, while the median expected probability of sea urchin mass mortality (P_m) following a tropical cyclone has not increased since 1980, storms with the greatest P_m have increased over the past 30 yr (Fig. 3). This is indicated by the increasing slope of P_m with the increase in quantile. The 95th quantile has a slope of $2.4\% \text{ yr}^{-1}$ compared to a slope of near zero for median values of P_m . Our analysis also showed that the median distance of storms from the Nova Scotian coast has decreased significantly by 9 km yr^{-1} , or 270 km since 1980 (Fig. 4A,D). This increased proximity to the coast is especially pronounced for storms in the upper quantiles (60th to 80th), since a storm's distance from the coast is bounded at zero. We also found that, while maximum sustained wind speed of tropical cyclones, on average, has not increased over the last 30 yr, the strongest

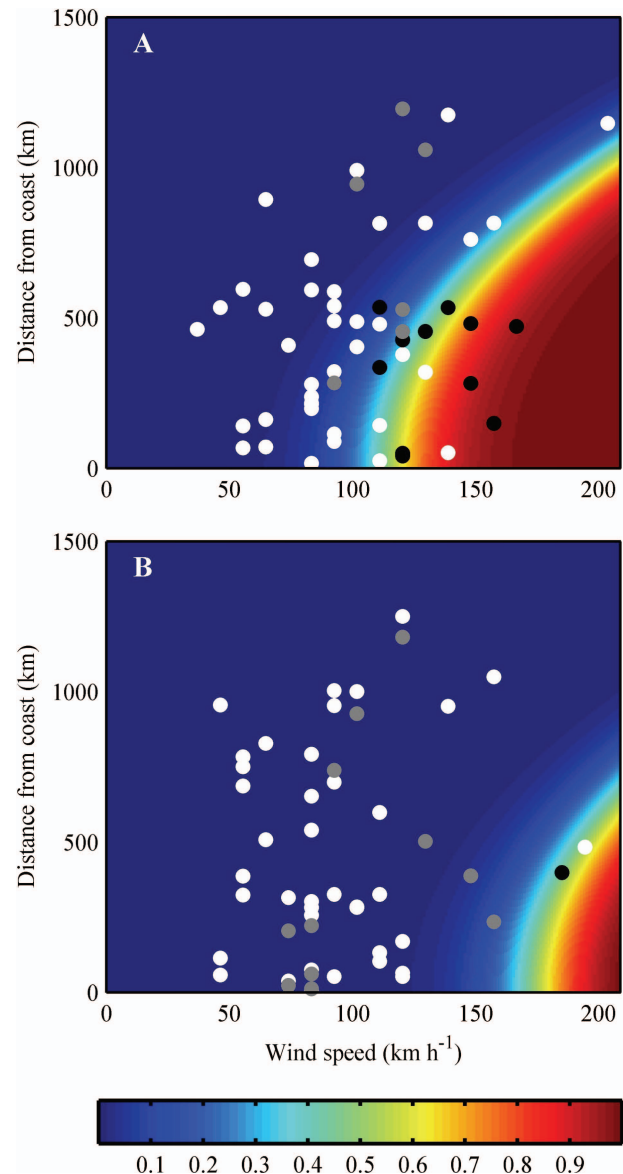


Fig. 2. Predicted probability (color spectrum), based on logistic regression, of mass mortality of sea urchins associated with tropical cyclones as a function of minimum distance from the Atlantic coast of Nova Scotia and maximum sustained wind speed at that time, for storms followed by average ocean temperatures (0–10-m depth) (A) above or (B) below a temperature threshold (12.2°C). Black dots are candidate storms that are most likely associated with mass mortality in a given year. White dots are storms not associated with a mass mortality. Gray dots are storms occurring after the candidate storm or onset of mass mortality, and are not included in our analysis.

storms (above the 80th quantile) tended to increase in intensity (Fig. 4B,E).

Average water temperature after the passage of a storm has increased significantly since 1980 (Fig. 4C,F), with lower temperatures becoming warmer at a rate of 0.1°C to $0.2^\circ\text{C yr}^{-1}$ (Fig. 4F). Average coastal water temperature between August and November also increased significantly during this 30-yr period by $0.07^\circ\text{C yr}^{-1}$ (Fig. 5).

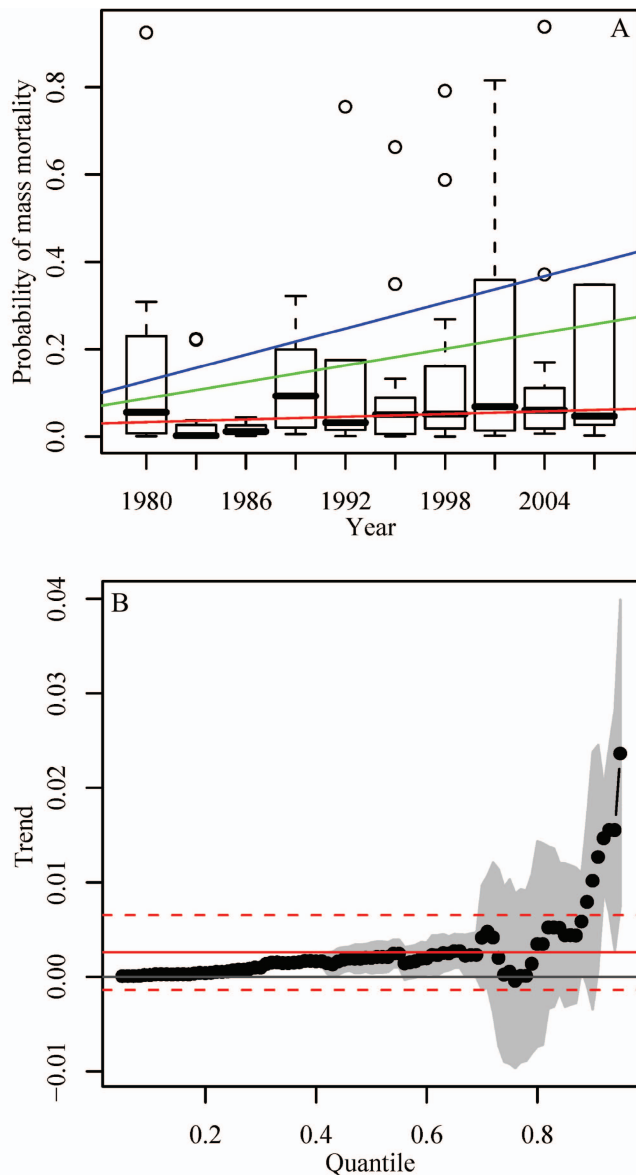


Fig. 3. (A) Box plot of probability of mass mortality of sea urchins associated with tropical cyclones off Nova Scotia between 1980 and 2009. Storms are grouped in 3-yr periods to increase the sample size within each bin ($n = 5-16$). Trend lines are shown for the median (red), 75th quantile (green), and 1.5 times the interquartile range (blue). (B) Trend in quantile values of the probability of mortality associated with storms in (A). Black dots represent the mean slope estimate, and the gray band represents the 90% confidence intervals (CI). Solid red line shows the least-square regression slope estimate, and dashed lines show the 90% CI.

Discussion

Our logistic regression model showed that tropical storm intensity and proximity to the coast were important predictors of mass mortality of sea urchins. The 12.2°C threshold temperature that provides the best fit of our model approximates the threshold for progression or transmission of paramoebiasis (between 10°C and 12°C),

based on laboratory studies (Scheibling and Stephenson 1984). Storms occurring later in the season that have a high P_m , based on their proximity to the coast and wind strength, are less likely to result in morbidity or mortality if they occur when temperatures are at or below 12.2°C and dropping (Scheibling et al. 2010).

The potential for tropical cyclones to deliver a non-indigenous pathogen to Nova Scotia will depend on spatial scale of wind-generated turbulent mixing. The importance of wind speed and proximity of storms along this coast as predictors of the probability of mass mortality reflects this potential. Empirical observations of changes in surface temperature and currents obtained from moored oceanographic platforms (Dickey et al. 1998) and computer simulations of coupled ocean-atmosphere models (Korty et al. 2008; Liu et al. 2008; Zedler 2009) indicate that wind-generated turbulent mixing can extend for 400–800 km across the wake of a strong hurricane. The average distance from the coast of our candidate storms (346.7 km) lies well within this range, although by the time these hurricanes reached the Scotian Shelf they generally had decreased in intensity.

Source populations of *P. invadens* that infect sea urchins in Nova Scotia are unknown. Negative growth of the amoeba in culture at 2°C suggests it is not indigenous to the Atlantic coast, where ocean temperature drops below 0°C in winter (Scheibling and Hennigar 1997; Jellett and Scheibling 1988). Cultured amoebae do not survive at 27°C, ruling out the possibility of a tropical origin for this species or its transport via the Gulf Stream (Jellett and Scheibling 1988), although mesoscale eddies (warm-core rings) that form along the northern boundary of the Gulf Stream can entrain Scotian Shelf water, and these features may interact with passing storms to spread the pathogen coastward (Scheibling and Hennigar 1997). Species of *Paramoeba* have been identified as causative agents of disease in crabs and lobsters (Newman and Ward 1973; Mullen et al. 2004) in the northeastern United States. In the fall of 1999, dead or dying crabs and sea urchins were reported in Long Island Sound during a mass mortality of lobster attributed to paramoebiasis (Mullen et al. 2004). The concurrence of these events and widespread sea urchin mortality in Nova Scotia in October following Hurricane Danielle (*see* Web Appendix) suggests a possible source region for *Paramoeba* along the eastern seaboard of the United States. Another possibility is that deep-dwelling populations of *P. invadens* in sedimentary habitats on the Scotian Shelf are mixed into the water column with the passing of major storms. *Paramoeba* is found in marine sediments, and these populations may be resistant to low temperature, perhaps in a cyst form (Jellett and Scheibling 1988; Jellett et al. 1989).

Our trend analysis showed that the likelihood of storms with the greatest P_m has increased over the past 30 yr. In other words, the most deadly storms, in terms of the potential for sea urchin mortality, have become more deadly. This is consistent with the observed increase in the occurrence of mass mortality events between the first (five mass mortalities, including 1983) and second half (eight mass mortalities) of our study period. We also found that

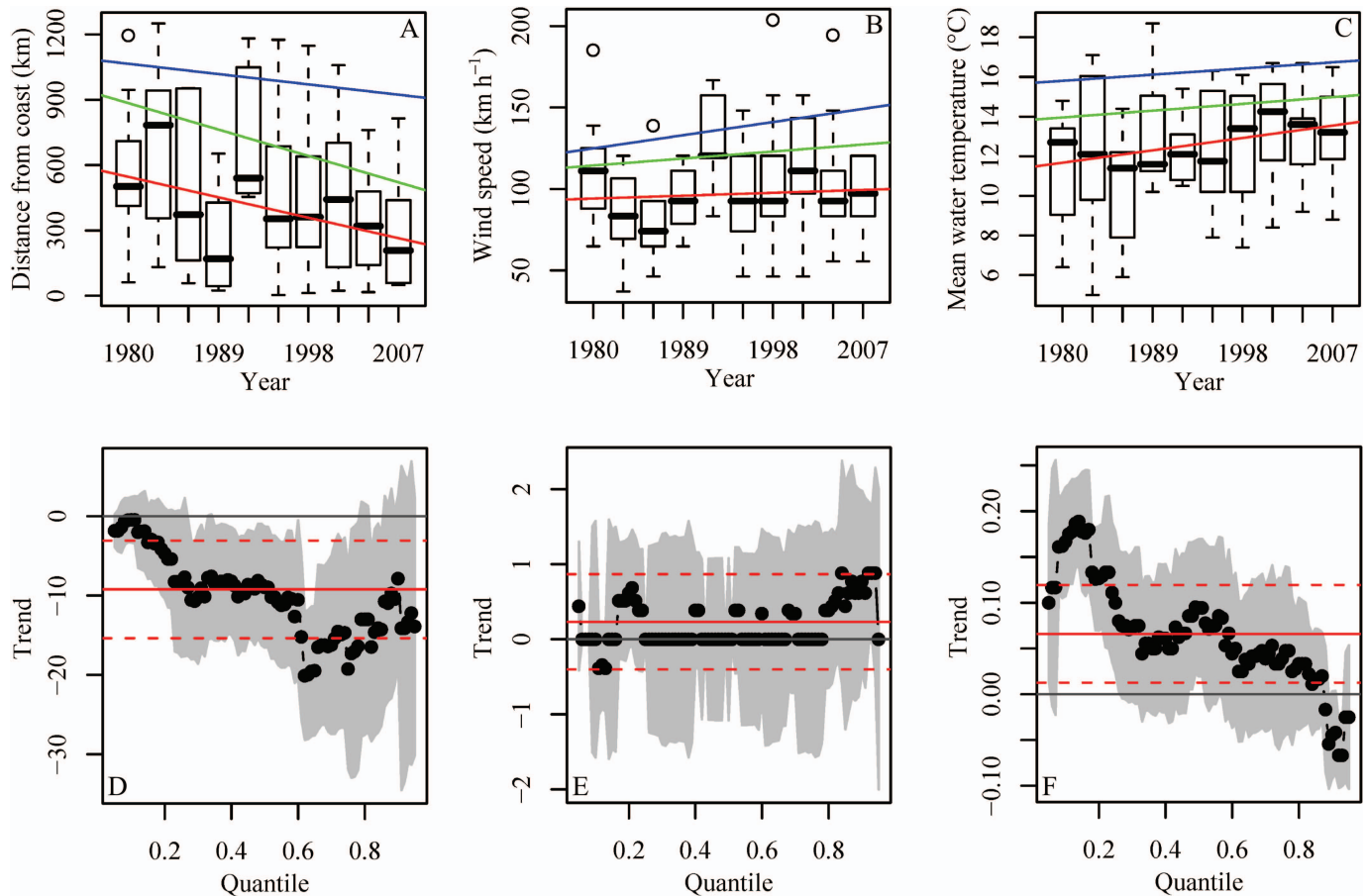


Fig. 4. (A) Box plot of closest distance from coast, (B) maximum sustained wind speed, and (C) 2-week poststorm average water temperature for tropical cyclones off Nova Scotia between 1980 and 2009. Storms are grouped in 3-yr periods to increase the sample size within each bin. Trend lines are shown for the median (red), 75th quantile (green), and 1.5 times the interquartile range (blue). (D) Trends in the quantile values of closest distance from coast, (E) maximum sustained wind speed, and (F) poststorm average water temperature for all storms. Black dots represent the mean slope estimate, and the gray band represents the 90% CI. Solid red line shows the least-square regression slope estimate, and dashed lines show the 90% CI.

the strongest storms tended to increase in intensity and proximity to the coast. If storm-generated currents are carrying *P. invadens*, these trends likely will increase the probability that the pathogen will be introduced to shallow-dwelling sea urchin populations.

Average water temperature after the passage of a storm also has increased since 1980, as lower temperatures have become warmer. This trend is likely to increase the probability of sea urchin mass mortality because fewer storms will arrive when water temperature is below the thermal threshold for disease propagation. The rate of increase in average coastal water temperature between August and November over the past 30 yr ($0.07^{\circ}\text{C yr}^{-1}$) exceeds that reported for the same period in the Northern Hemisphere ($0.02^{\circ}\text{C yr}^{-1}$; Trenberth et al. 2007). An increase in the intensity of the strongest hurricanes has been linked to ocean warming in the North Atlantic and elsewhere (Emanuel 2005; Elsner et al. 2008). This trend is expected to continue with a doubling of the frequency of category 4 and 5 storms over the next century (Bender et al. 2010).

If our trend analysis and current hurricane predictions hold true, our model predicts an increase in the likelihood of delivery of the pathogenic agent to the coast of Nova Scotia, due to changes in intensity or trajectory of tropical storms in the North Atlantic, or to increases in ocean surface temperatures during the hurricane season. Whether a mass mortality event occurs following the introduction of *P. invadens* to the coast, and the spatial extent of that mortality, will depend on the distribution and abundance of shallow-water (< 25-m depth) sea urchin populations. Laboratory experiments have shown that the rate of water-borne transmission of paramoebiasis is density-dependent (Scheibling and Stephenson 1984), and host density has been linked to disease outbreaks in other sea urchin species (Lafferty 2004). In the 1980s and early 1990s, high densities of sea urchins occurred in extensive barrens along the Atlantic coast of Nova Scotia. The increased frequency of mass mortality events in the late 1990s and 2000s has decimated these populations. Following the last major die-off in 1999, sea urchins have been slow to repopulate shallow subtidal habitats, and their present distribution is

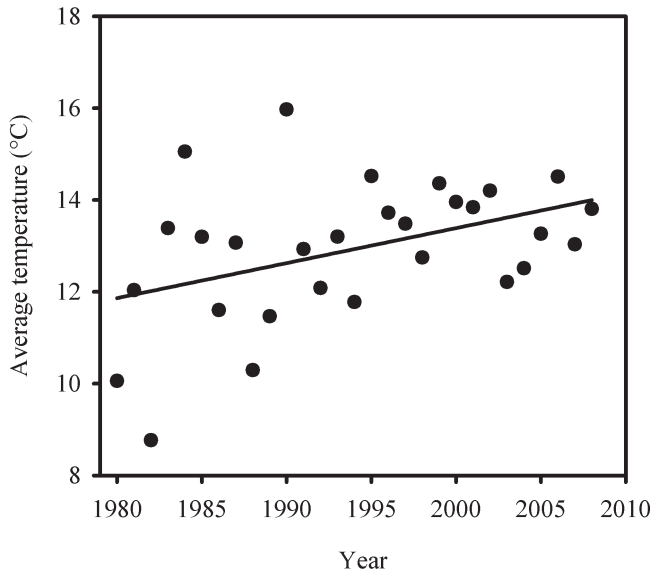


Fig. 5. Average water temperature (0–10-m depth) along the Atlantic coast of Nova Scotia between August and November 1980 and 2008. Line represents the linear regression of average temperature against year ($r^2 = 0.18$, $F_{1,27} = 5.822$, $p = 0.023$); slope = $0.0762^\circ\text{C yr}^{-1} \pm 0.0316$ SE.

largely localized to the headland west of Halifax Harbour (Brady and Scheibling 2005; Lauzon-Guay and Scheibling 2007). Although the potential for delivery of the pathogen may be increasing, the frequency of future disease outbreaks likely will be limited by the range and density of the susceptible host population.

Recurrent introductions of a pathogenic agent with the potential to cause mass mortality of sea urchins will ultimately disrupt the historical cycling between alternative states of the subtidal ecosystem in Nova Scotia (Lauzon-Guay et al. 2009). After sea urchin mass mortality, reduction in grazing pressure results in a phase shift to kelp beds. These highly productive algal habitats persist until sea urchins again increase in abundance, through recruitment or migration from refuge populations in deeper, colder waters (below the thermal threshold for paramoebiasis), and form destructive grazing aggregations that drive the transition back to sea urchin barrens (Scheibling et al. 1999; Lauzon-Guay et al. 2009). We predict that the increased frequency of disease outbreaks, by limiting the resilience of sea urchin populations in shallow habitats, will maintain the ecosystem in the kelp bed state. This could benefit lobster and finfish fisheries that rely on kelp beds as nursery habitat and a major source of primary production for benthic food webs (Wharton and Mann 1981). On the other hand, recurrent mass mortality of *S. droebachiensis* has already caused the collapse of the sea urchin fishery in Nova Scotia (Miller and Nolan 2008), and there is little prospect for recovery on a coastal scale.

Acknowledgments

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References

- BENDER, M. A., T. R. KNUTSON, R. E. TULEYA, J. J. SIRUTIS, G. A. VECCHI, A. T. GARNER, AND I. M. HELD. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science* **327**: 454–458, doi:10.1126/science.1180568
- BRADY, M. S., AND R. E. SCHEIBLING. 2005. Repopulation of the shallow subtidal zone by green sea urchins (*Strongylocentrotus droebachiensis*) following mass mortality in Nova Scotia, Canada. *J. Mar. Biol. Assoc. U.K.* **85**: 1511–1517, doi:10.1017/S0025315405012713
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag.
- DICKEY, T., AND OTHERS. 1998. Upper-ocean temperature response to Hurricane Felix as measured by the Bermuda testbed mooring. *Mon. Weather Rev.* **126**: 1195–1201, doi:10.1175/1520-0493(1998)126<1195:UOTRTH>2.0.CO;2
- ELSNER, J. B., J. P. KOSSIN, AND T. H. JAGGER. 2008. The increasing intensity of the strongest tropical cyclones. *Nature* **455**: 92–95, doi:10.1038/nature07234
- EMANUEL, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* **436**: 686–688, doi:10.1038/nature03906
- HARVELL, C. D., C. E. MITCHELL, J. R. WARD, S. ALTIZER, A. P. DOBSON, R. S. OSTFELD, AND M. D. SAMUEL. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* **296**: 2158–2162, doi:10.1126/science.1063699
- , AND OTHERS. 1999. Emerging marine diseases—climate links and anthropogenic factors. *Science* **285**: 1505–1510, doi:10.1126/science.285.5433.1505
- HUGHES, T. P. 1999. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**: 1547–1551, doi:10.1126/science.265.5178.1547
- JELLETT, J. F., J. NOVITSKY, J. CANTLEY, AND R. E. SCHEIBLING. 1989. Non-occurrence of *Paramoeba invadens* in the water column and sediments off Halifax, Nova Scotia. *Mar. Ecol. Prog. Ser.* **56**: 205–209, doi:10.3354/meps056205
- , AND R. E. SCHEIBLING. 1988. Effect of temperature and food concentration on the growth of *Paramoeba invadens* (Amoebida: Paramoebidae) in monoxenic culture. *Appl. Environ. Microbiol.* **54**: 1848–1854.
- JONES, G. M., AND R. E. SCHEIBLING. 1985. *Paramoeba* sp. (Amoebida, Paramoebidae) as the possible causative agent of sea urchin mass mortality off Nova Scotia. *J. Parasitol.* **71**: 559–565, doi:10.2307/3281424
- KOENKER, R. 2005. Quantile regression. Cambridge Univ. Press.
- KORTY, R. L., K. A. EMANUEL, AND J. R. SCOTT. 2008. Tropical cyclone-induced upper-ocean mixing and climate: Application to equable climates. *J. Clim.* **21**: 638–654, doi:10.1175/2007JCLI1659.1
- LAFFERTY, K. D. 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecol. Appl.* **14**: 1566–1573, doi:10.1890/03-5088
- , J. W. PORTER, AND S. FORD. 2004. Are diseases increasing in the ocean? *Annu. Rev. Ecol. Evol. Syst.* **35**: 31–54, doi:10.1146/annurev.ecolsys.35.021103.105704

- LAUZON-GUAY, J.-S., AND R. E. SCHEIBLING. 2007. Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (*Strongylocentrotus droebachiensis*) in relation to wave action and sea temperature. *Mar. Biol.* **151**: 2109–2118, doi:10.1007/s00227-007-0668-2
- , ———, AND M. A. BARBEAU. 2009. Modelling phase shifts in a rocky subtidal ecosystem. *Mar. Ecol. Prog. Ser.* **375**: 25–39, doi:10.3354/meps07758
- LESSIOS, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annu. Rev. Ecol. Syst.* **19**: 371–393.
- LIU, L. L., W. WANG, AND R. X. HUANG. 2008. The mechanical energy input to the ocean induced by tropical cyclones. *J. Phys. Oceanogr.* **38**: 1253–1266, doi:10.1175/2007JPO3786.1
- MCCALLUM, H., D. HARVELL, AND A. DOBSON. 2003. Rates of spread of marine pathogens. *Ecol. Lett.* **6**: 1062–1067, doi:10.1046/j.1461-0248.2003.00545.x
- MILLER, R. J. 1985a. Succession in sea urchin and seaweed abundance in Nova Scotia, Canada. *Mar. Biol.* **84**: 275–286, doi:10.1007/BF00392497
- . 1985b. Sea urchin pathogen: A possible tool for biological control. *Mar. Ecol. Prog. Ser.* **21**: 169–174, doi:10.3354/meps021169
- , AND S. C. NOLAN. 2008. Management methods for a sea urchin dive fishery with individual fishing zones. *J. Shellfish Res.* **27**: 929–938, doi:10.2983/0730-8000(2008)27[929:MMFASU]2.0.CO;2
- MULLEN, T. E., AND OTHERS. 2004. Paramoebiasis associated with mass mortality of American lobster *Homarus americanus* in Long Island Sound, USA. *J. Aquat. Anim. Health* **16**: 29–38, doi:10.1577/H02-045.1
- MYDLARZ, L. D., L. E. JONES, AND C. D. HARVELL. 2006. Innate immunity, environmental drivers, and disease ecology of marine and freshwater invertebrates. *Annu. Rev. Ecol. Syst.* **37**: 251–288, doi:10.1146/annurev.ecolsys.37.091305.110103
- NEWMAN, M. W., AND G. E. WARD. 1973. An epizootic of blue crabs, *Callinectes sapidus*, caused by *Paramoeba pernisciosa*. *J. Invertebr. Pathol.* **22**: 329–334, doi:10.1016/0022-2011(73)90159-6
- ROBERTS-REGAN, D. L., R. E. SCHEIBLING, AND J. F. JELLETT. 1988. Natural and experimentally induced lesions of the body wall of sea urchins (*Strongylocentrotus droebachiensis*). *Dis. Aquat. Org.* **5**: 51–62, doi:10.3354/dao005051
- SCHEIBLING, R. E., C. M. FEEHAN, AND J.-S. LAUZON-GUAY. 2010. Disease outbreaks associated with recent hurricanes cause mass mortality of sea urchins in Nova Scotia. *Mar. Ecol. Prog. Ser.* **408**: 109–116, doi:10.3354/meps08579
- , AND A. W. HENNIGAR. 1997. Recurrent outbreaks of disease in sea urchins *Strongylocentrotus droebachiensis* along the Atlantic coast of Nova Scotia: Evidence for a link with large-scale meteorologic and oceanographic events. *Mar. Ecol. Prog. Ser.* **152**: 155–165, doi:10.3354/meps152155
- , ———, AND T. BALCH. 1999. Destructive grazing, epiphytism, and disease: The dynamics of sea urchin-kelp interactions in Nova Scotia. *Can. J. Fish. Aquat. Sci.* **56**: 2300–2314, doi:10.1139/cjfas-56-12-2300
- , AND R. L. STEPHENSON. 1984. Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. *Mar. Biol.* **78**: 153–164, doi:10.1007/BF00394695
- TAJIMA, K., AND J. M. LAWRENCE. 2001. Disease in sea urchins, p. 167–190. *In* J. M. Lawrence [ed.], *Edible sea urchins: Biology and ecology*. Elsevier Science.
- TRENBERTH, K. E., AND OTHERS. 2007. Observations: Surface and atmospheric climate change, p. 235–336. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller [eds.], *Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change*. Cambridge Univ. Press.
- UTHICKE, S., B. SCHAFFELKE, AND M. BYRNE. 2009. A boom and bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecol. Monogr.* **79**: 3–24, doi:10.1890/07-2136.1
- WARD, J. R., AND K. D. LAFFERTY. 2004. The elusive baseline of marine disease: Are diseases in ocean ecosystems increasing? *PLoS. Biol.* **2**: 542–547.
- WHARTON, W. G., AND K. H. MANN. 1981. Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. *Can. J. Fish. Aquat. Sci.* **38**: 1339–1349, doi:10.1139/f81-180
- ZEDLER, S. E. 2009. Simulations of the ocean response to a hurricane: Nonlinear processes. *J. Phys. Oceanogr.* **39**: 2618–2634, doi:10.1175/2009JPO4062.1

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